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Combining local and global contributions to perceived colour: An analysis of the variability in symmetric and asymmetric colour matching

Eli Brenner *, Jeroen J.M. Granzier, Jeroen B.J. Smeets

Faculty of Human Movement Sciences, Vrije Universiteit, Van der Boechorststraat 9, 1081 BT Amsterdam, The Netherlands

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Abstract

Are surfaces' colours judged from weighted averages of the light that they reflect to the eyes and the colour contrast at their borders? To find out we asked subjects to set the colour and luminance of test disks to match reference disks, on various backgrounds, and analysed the variability in their settings. Most of the variability between repeated settings was in luminance. The standard deviations in the set colour were smallest when the disk and background were the same colour, irrespective of the colour itself. Matches were equally precise for greenish or reddish disks on a grey background, as for grey disks on a greenish or reddish background. The precision was less dependent on the colour contrast at the disks' borders when the backgrounds were more complex and when there was a large luminance contrast at the disks' borders. Subjects were less precise when different colours surrounded the two disks. These findings are consistent with the perceived colour at any position being a weighted average of the local cone excitation ratio and the change in the cone excitation ratio at the borders of the surface in question. However, the involved weights must be variable and depend systematically on parameters such as the luminance contrast at the surface's borders and other chromatic contrasts within the scene.

Keywords: Colour constancy; Colour vision; Chromatic induction; Variability

1. Introduction

When we compare surfaces' colours we are actually comparing the light that these surfaces reflect to the cones in our eyes, and in particular the relative responses of cones with different spectral sensitivities to stimulation by the light from the surfaces in question. The response of each kind of cone depends on the colour and intensity of the light falling on it, and thus both on surface reflectance and on the colour and intensity of the illumination. The ratio between the stimulation of two kinds of cones (which we will refer to as a local cone ratio; **L**, the precise definition of which will be given in Section 2) depends on the colour of the light but not on its intensity, so it is independent of the intensity of the illumination. The ratio between the local cone ratios at two sides of the border between two surfaces (which we will refer to as the border ratio; **B**, see Section 2) even hardly depends on the colour of the illumination (Foster & Nascimento, 1994; Foster et al., 1997; Land & McCann, 1971). However, although relying on border ratios would make judgments of surfaces' colours much less sensitive to the colour of the illumination (Land, 1983), it would make the judgments depend on the colour of surrounding surfaces (Brenner & Cornelissen, 1991). To avoid excessive influences of the direct surrounding one could consider differences between cone-ratios throughout the scene (or in relation to the brightest surface in the scene), but this is only expected to result in better estimates if there is no overall bias in chromaticity within the scene and the illumination is more or less uniform.

* Corresponding author.
E-mail address: e.brenner@fbw.vu.nl (E. Brenner).

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Moreover, most studies that examined this option found a negligible influence of the number of surfaces within a scene on colour judgments (Amano, Foster, & Nascimento, 2005; Brenner, Cornelissen, & Nuboer, 1989; Nascimento, de Almeida, Fiadeiro, & Foster, 2005; Valberg & Lange-Malecki, 1990; Yund & Armington, 1975). So is a surface's apparent colour determined by a compromise between the local cone ratio and the average border ratio?

The modest but consistent influence of surrounding colours on judgments of a surface's colour (e.g. Brenner, Ruiz, Herraiz, Cornelissen, & Smeets, 2003; Delahunt & Brainard, 2004; Jameson & Hurvich, 1961; Kirschmann, 1891; Land, 1986; Walraven, 1973) is consistent with such a compromise. However a surface's apparent colour does not *only* depend on the local cone ratio and the border ratio, because there are conditions in which other surfaces' colours matter (e.g. Barnes, Wei, & Shevell, 1999; Brenner et al., 2003; Kraft & Brainard, 1999; Shevell & Wei, 1998; Wachtler, Albright, & Sejnowski, 2001). Eye movements could mediate some additional influences of more remote surfaces by providing the opportunity to directly compare successively fixated surfaces and by influencing the cones' states of adaptation (Cornelissen & Brenner, 1995), but this cannot account for all of the effects that have been found. We propose that further effects are mediated by changes in the weights given to the local cone ratio and the border ratio, which depend on the chromatic and luminance contrast within the surrounding image.

In order to evaluate this proposal we examine the variability in symmetric and asymmetric colour matching. We expect patterns in the variability to provide information about the underlying mechanisms. To explain how, we first discuss a related, well-established example. Reddish colours are distinguished from greenish ones on the basis of the ratio between the stimulation of two kinds of cones, that are often referred to as of *l*- and *m*-cones. The range of ratios that one needs to deal with is quite limited, because the cones' spectral sensitivities are broad and largely overlap (as are and do the spectra of most light sources and the spectral reflectance of most surfaces). In contrast, the range of encountered sums of the stimulation of *l*- and *m*-cones is large. So if these ratios (colour) and sums (luminance) are determined in the retina (Lee, 1996; Lennie & D'Zmura, 1988; Pokorny & Smith, 1986), before the resolution within the colour and luminance channels is limited by the maximal firing rate of retinal ganglion cells, most resolution will be lost in conveying information about the sums. And indeed, Noorlander, Heuts, and Koenderink (1981) have shown that larger (low temporal frequency) modulations in the stimulation of two kinds of cones go by undetected when the cones are modulated in phase (giving fluctuations in luminance) than when they are modulated out of phase (giving fluctuations in colour).

Following a similar line of reasoning we expect to see differences in matching precision for different combinations of targets and backgrounds. If border ratios (**B**) play an important role in evaluating the targets' colours (mediated for instance by double-opponent colour cells in V1; Conway, Hubel, & Livingstone, 2002), one can expect matches to become less precise as we increase the difference in colour between the target and the background (Sankeralli & Mullen, 1999; Sankeralli, Mullen, & Hine, 2002). If only local cone ratios (**L**) are important, we expect to see no effect of background colour. Thus the extent to which the precision depends on the background can be used as a measure of the relative weight given to **B** rather than **L**.

In the present study, we compare the variability in colour matches for various combinations of reference target colour and background colour. We introduce a simplistic model to evaluate the credibility of the hypothesis that colours are judged from a weighted average of the light from the surface itself (**L**) and the colour contrast at its borders (**B**). We examine whether such a model can more or less fit the data, and if so whether the weights given to **L** and **B** depend on the kind of background (complexity; luminance contrast; symmetric or asymmetric) in a reasonable manner.

2. Methods

Eight subjects took part in the experiment including the authors. The stimuli were computer-generated images presented on a 48 by 31 cm CRT screen (resolution: 1920 by 1200 pixels; 90 Hz). Subjects sat 2 m from the screen. The room was dark except for the light from the screen. In their first session, subjects were presented with an isolated 2° diameter disk at the centre of the screen. Its luminance was 20 cd/m^2. They could adjust the disk's colour (within the range that could be rendered at this luminance) by moving the computer mouse. They were asked to set the disk to appear to be grey (achromatic). The colour that they indicated was used as a starting point for constructing all the subsequent stimuli (including those in the following sessions). After this initial setting subjects always saw two 2° diameter disks, side by side, with a distance of 5° (or in one session sometimes 3° or 9°) between their centres (Fig. 1).

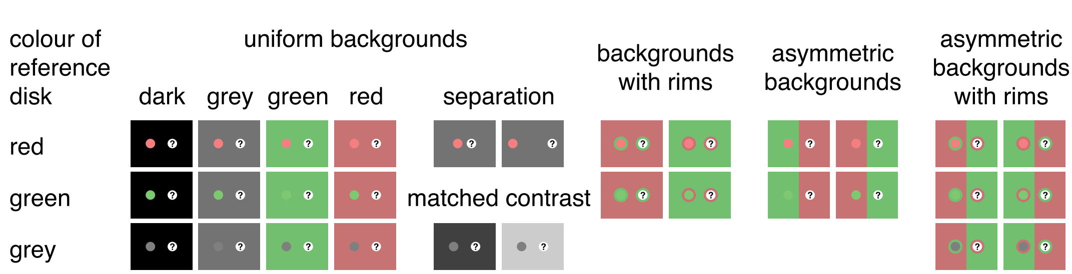

Fig. 1. The images in the 30 different conditions. Subjects set the colour and luminance of the disk on the right (indicated by the question mark) to match the reference disk on the left. (For interpretation of colour mentioned in this figure the reader is referred to the web version of the article.)

2.1. The reference

The disk on the left was the reference. It could either be grey (as indicated by the individual subject in the manner described above), or it could be reddish or greenish. The reddish colour stimulated the *l*-cones 10% more than the grey does, while stimulating the *m*- and *s*-cones to exactly the same extent as the grey does. The greenish colour stimulated the *l*-cones 10% less than the grey does. Thus for the *m*- and *s*-cones the three reference colours were identical; but they differed for the *l*-cones. Consequently, the luminance of the reference depended on its colour: the redder the reference the brighter it was.

2.2. Matching the reference

Subjects set the colour of the disk on the right (indicated by question marks in the figures) to match the reference. They adjusted its colour by moving the computer mouse. They could increase the *l*-cone stimulation by moving the mouse to the right, which made the disk look redder and brighter. They could decrease the *l*-cone stimulation by moving the mouse to the left, which made the disk look greener and darker. They could decrease the *m*-cone stimulation by moving the mouse towards their body, which made the disk look redder and darker. They could increase the luminance by moving the mouse away and to the right to increase the stimulation of both *l*- and *m*-cones. And so on. A linear mouse displacement resulted in a logarithmic change in cone stimulation. Thus the computer mouse can be considered to navigate within a logarithmic *l*–*m*-cone-stimulation colour space. This is also the colour space in which we present and analyse our data, because the data are more or less normally distributed in this colour space (Fig. 2). In this colour space, equal changes in cone stimulation ratio (i.e. equal differences between log cone stimulation) are represented by equal distances. The *s*-cone stimulation was constant: it was fixed at the correct value for a perfect match. This implies that increasing *l*- and *m*-cone stimulation together makes the target both brighter and more yellow; while decreasing them together makes the target look darker and bluer. Thus what we call the luminance direction in our colour space (see Fig. 2) is actually a combination of luminance and yellow–blue colour opponency, whereas the colour direction only refers to red–green opponency. Subjects had to match the reference in both colour and brightness. The disk's initial colour was randomised for each trial.

2.3. The background

The background filled the screen and was designed in the same way as the reference, again using the same three colours, but based on a grey field that was 10% darker than the grey reference (18 cd/m^2 instead of 20 cd/m^2; unless stated otherwise). Again, reddish and greenish colours only differed from grey by giving a 10% stronger or weaker stimulation of the *l*-cones. Beside these three colours we also used a dark grey background (2 cd/m^2), and two backgrounds with identical contrast with the reference, but one had about twice the luminance of the reference whereas the other had about half its luminance. There were four kinds of backgrounds: a background filled with a single colour (*uniform background*), a background with a single colour except for an 0.5° wide rim of a different colour surrounding the two disks (*background with rim*), a background split horizontally into two equal parts with different colours (*asymmetric background*), and a split background with an 0.5° rim surrounding the disks (*asymmetric background with rim*).

2.4. Procedure

Each subject took part in 6 sessions. The first two sessions were identical (leftmost group of conditions in Fig. 1): subjects made symmetric colour matches on a uniform background for all 12 combinations of the three reference colours (grey, reddish and greenish) and four background colours (grey, reddish, greenish and dark grey). In each session they matched 10 references for each combination, giving a total of 20 matches for each of the 12 conditions. In the other four sessions subjects made 20 matches for each condition. In one session we compared two conditions with reddish disks on a grey background, but with different distances between the disks (3° or 9° between their centres; 1° or 7° between their closest edges). In that session we also compared two conditions with the same contrast between the grey reference and the uniform grey

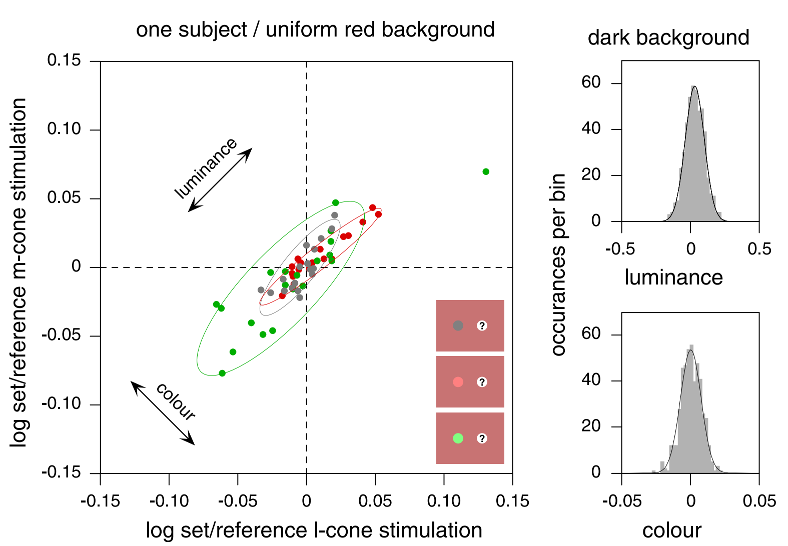

Fig. 2. (Left) One subject's settings for the three conditions with a uniform red background. The subject set the *l*- and *m*-cone stimulations of the disk on the right to match the grey, red or green disk on the left. Ellipses indicate 2 standard deviations (ignoring the green point at the upper right which was recognised to be an outlier by the procedure described in the methods section). (Right) Histograms of the errors in the colour (bottom) and luminance (top) directions indicated in the left panel, for matches made on a uniform dark background (combined data for 8 subjects in three conditions). Note that the errors are approximately normally distributed when represented in this manner (compare histograms with curves) and about 10 times as large in the luminance than in the colour direction (compare scales). (For interpretation of colour mentioned in this figure the reader is referred to the web version of the article.)

background, but the background was either darker or brighter than the reference (about 10 and 40 cd/m^2, respectively). In another session we separated the overall dominant colour in the scene from the contrast at the (reddish or greenish) disks' borders by surrounding the disks with greenish rims when the rest of the background was reddish, and vice versa. In the last two sessions, the disk of which the colour and luminance had to be set was on a greenish background if the reference was on a reddish one, and vice versa (asymmetric matching). For asymmetric matching without a rim the reference could either be red or green. For asymmetric matching with a rim (of the opposite colour than the rest of the background at that side) the reference could also be grey.

2.5. Analysis

The first step in the analysis was to examine the distribution of the errors. We did so by plotting the errors (for each subject in each condition) in the above-mentioned relative cone stimulation space: log l-cone stimulation versus log m-cone stimulation (with a perfect setting as the origin). We fit ellipses to these points by calculating the eigenvectors of the covariance matrix, determining the standard deviations along the directions of these eigenvectors, and using these standard deviations as the major and minor axes of the ellipses (in Fig. 2 each axis is 4 standard deviations long, so that the area within the ellipse represents a confidence interval of 2 standard deviations). Points were considered to be outliers if they were more than 4 standard deviations from the mean of the distribution of all the other points, with the standard deviation in the direction of the point in question being determined from the ellipses. This procedure for finding (and eliminating) outliers was applied to each point, and was iterated until no more outliers were found.

After removing outliers we determined the variability in luminance and the variability in colour, the former being the common variability in both cones and the latter the change in the cone ratio (corresponding with variability in the two diagonal directions in Fig. 2). Although our main interest is in the standard deviation in the matched colour, we also determined the standard deviation in luminance and the systematic errors in both measures. For asymmetric matching the systematic errors also give us a direct measure of the weight given to border ratios. All measures were determined for each of the 8 individual subjects and then averaged across subjects.

2.6. Modelling the data

In the introduction, we proposed that the apparent colour of a surface (**C**) is a weighted average of the local cone ratio (**L**) and the border ratio (**B**)

$$\mathbf{C} = w\mathbf{B} + (1-w)\mathbf{L}_{\mathrm{target}} \tag{1}$$

where the weight (w) given to the border ratio depends on the structure of the background (so that it can differ between conditions), and

$$\mathbf{L}_{\mathrm{target}} = \log\left(\frac{\boldsymbol{l}\ \text{cone stimulation}_{\mathrm{target}}}{\boldsymbol{m}\ \text{cone stimulation}_{\mathrm{target}}}\right)$$

and

$$\mathbf{B} = \log\left(\frac{\boldsymbol{l}\ \text{cone stimulation}_{\mathrm{target}}}{\boldsymbol{m}\ \text{cone stimulation}_{\mathrm{target}}}\Big/\frac{\boldsymbol{l}\ \text{cone stimulation}_{\mathrm{background}}}{\boldsymbol{m}\ \text{cone stimulation}_{\mathrm{background}}}\right) = \mathbf{L}_{\mathrm{target}} - \mathbf{L}_{\mathrm{background}}$$

The logarithm is introduced to make the values consistent with distances in our colour space, but it is irrelevant for the further reasoning and analysis.

Assuming that we have independent normally distributed variability in judgments of **L** and **B**, the expected variability (standard deviation; σ_C) in the perceived colour is:

$$\sigma_C = \sqrt{w^2\sigma_B^2 + (1-w)^2\sigma_L^2} \tag{2}$$

where σ_B is the standard deviation in **B**, and σ_L is the standard deviation in **L**.

Eqs. (1) and (2) apply to the perceived colour of a single surface. The standard deviation in subjects' settings is determined by the values of σ_C for both disks. Moreover, in Eq. (2) we assume that there is no variability in w. For symmetrical backgrounds, slight variability in the weights between repeated trials (but constant weights within trials) is expected to make very little difference, because it only affects the balance between the uncertainties in **L** and **B**. The perceived colour **C** will vary in the same way for both reference and test disks. However, for asymmetrical backgrounds, variability in w (σ_w) will result in different changes in the two disks. The additional variability can be written as $\sigma_w\Delta_{\mathrm{background}}$, where $\Delta_{\mathrm{background}}$ is the difference between the two background colours. All in all the standard deviation in the settings (σ_S) is therefore expected to be:

$$\sigma_S = \sqrt{w^2(\sigma^2_{B_{\mathrm{reference}}} + \sigma^2_{B_{\mathrm{set}}}) + (1-w)^2 2\sigma_L^2 + \sigma_w^2\Delta^2_{\mathrm{background}}} \tag{3}$$

The term σ_w disappears from the equation for symmetric backgrounds because for symmetric backgrounds $\Delta_{\mathrm{background}}$ is zero. Since our proposal is that **B** and **L** are determined locally, we must assume that σ_L and σ_B are independent of the rest of the scene, so we assume that the same values apply for the same colour of the disk (for σ_L), or combination of colours of the disk and background (for σ_B), for all conditions. Before fitting Eq. (3) to our data (by minimizing the sum of squares of the residuals of the fit) we made several additional assumptions to reduce the number of free parameters.

Although we realise that matches may be slightly more precise for less saturated colours, we assume that σ_L is independent of the colour of the reference disk (in accordance with our choice of colour space), making σ_L a single parameter in the fit. We assume that σ_B is proportional to the colour contrast itself ($\sigma_B = \alpha\mathbf{B}$; although again we realise that this may not be completely true), so that it too gives rise to a single fit parameter: the slope α of the relationship between **B** and σ_B. Thus, Eq. (3) can be rewritten as:

$$\sigma_S = \sqrt{w^2(\alpha^2\mathbf{B}^2_{\mathrm{reference}} + \alpha^2\mathbf{B}^2_{\mathrm{set}}) + (1-w)^2 2\sigma_L^2 + \sigma_w^2\Delta^2_{\mathrm{background}}} \tag{4}$$

We assume that the main thing that varies between the different kinds of scenes is the value of w. We assume that the value of w does not depend on the specific colours involved (which may not be completely true) and ignore the small differences in luminance between the disks and backgrounds as a result of only changing the l-cone stimulation. Thus, all in all we have six values of w: one for the uniform (18 cd/m^2) backgrounds, one for the uniform dark (2 cd/m^2) backgrounds, one for the two uniform backgrounds with matched contrast (which turn out to have similar variability), one for the backgrounds with rims, one for the asymmetric backgrounds, and one for the asymmetric backgrounds with rims. We estimate the values of w for the two kinds of asymmetric backgrounds directly from the average systematic errors in those two conditions, because our proposal is that the systematic errors (the phenomenon known as chromatic induction or simultaneous colour contrast) arise from relying on the border contrast. The magnitude of the systematic error is equal to $w\ \Delta_{\mathrm{background}}$.

We assume that σ_w depends on the value of w, so we take it to be independent of the colours of the disks and backgrounds (as we did for w), but fit separate values for scenes with and without a rim (for which we determined separate values of w). Thus, σ_L and α have a single value for all conditions and w has a different value for each of the four above-mentioned kinds of symmetric backgrounds. For the asymmetric backgrounds, w is determined by dividing the systematic error in the settings by the difference between the background colours ($\Delta_{\mathrm{background}}$). This gives a direct estimate of w because the systematic error introduced by differences in background colour is proportional to w (see Eq. (1)). For each of the two kinds of asymmetric backgrounds, the value of w was determined in this manner (averaged across target and background colours), and the value of σ_w was determined from the fit.

Since the purpose of the model (Eq. (4) with the associated assumptions) is to evaluate whether approaching colour vision as a weighted average of local and border contrast is feasible, rather than to provide a detailed description of human behaviour, we will not try to introduce more detail to the model, or to conduct statistical tests to examine whether we can reject the model as a perfect account of human performance. Instead we will examine whether the model fits the data globally, and if not we will discuss whether modifying some of our assumptions is likely to be enough for simulating human performance, or whether the idea underlying the model has to be rejected.

3. Results

3.1. Colour

On average, our subjects choose $\mathrm{CIE}_{x,y}$ coordinates (0.33, 0.36) as being a perfect grey, with a standard deviation between subjects of 0.02 for both coordinates. Altogether, 72 (1.5%) of the 4800 settings (8 subjects, 30 conditions, 20 replications) were excluded from further analysis because they were considered to be outliers. Fig. 2 shows one (naïve) subject's settings for the symmetrical matches on a red background. Settings for the three reference colours are represented by differently coloured symbols. The horizontal and vertical axes represent the deviations from a correct match for the *l*- and *m*-cones, respectively. Two things are evident from the distributions of the settings. First, that most of the variability is in luminance (maintaining the ratio of excitation of the *l*- and *m*-cones so that the ellipses have an orientation of about 45°). Second, that the variability in colour is larger for the greenish reference than for the reddish reference (for this subject and a reddish background).

Fig. 3 shows the average of all subjects' standard deviations in the colour direction (see Fig. 2) for each of the 30 conditions (solid symbols). The standard deviations in the direction of the minor axis of the fit ellipses are also shown for comparison (open symbols). The overall pattern in the way in which the standard deviation depends on the condition is about the same for both measures. By definition, the standard deviations along the minor axis of the fit ellipses are lower than those in the colour direction, but since the two values are about the same the variability in the matches must primarily be in luminance. From the pattern itself we can draw six conclusions.

First, it is evident that the colour contrast at the disks' borders is relevant. The smallest standard deviations (lowest values) are found for disks on a uniform background of the same colour as the reference. For disks on a uniform background, the largest standard deviations are found for

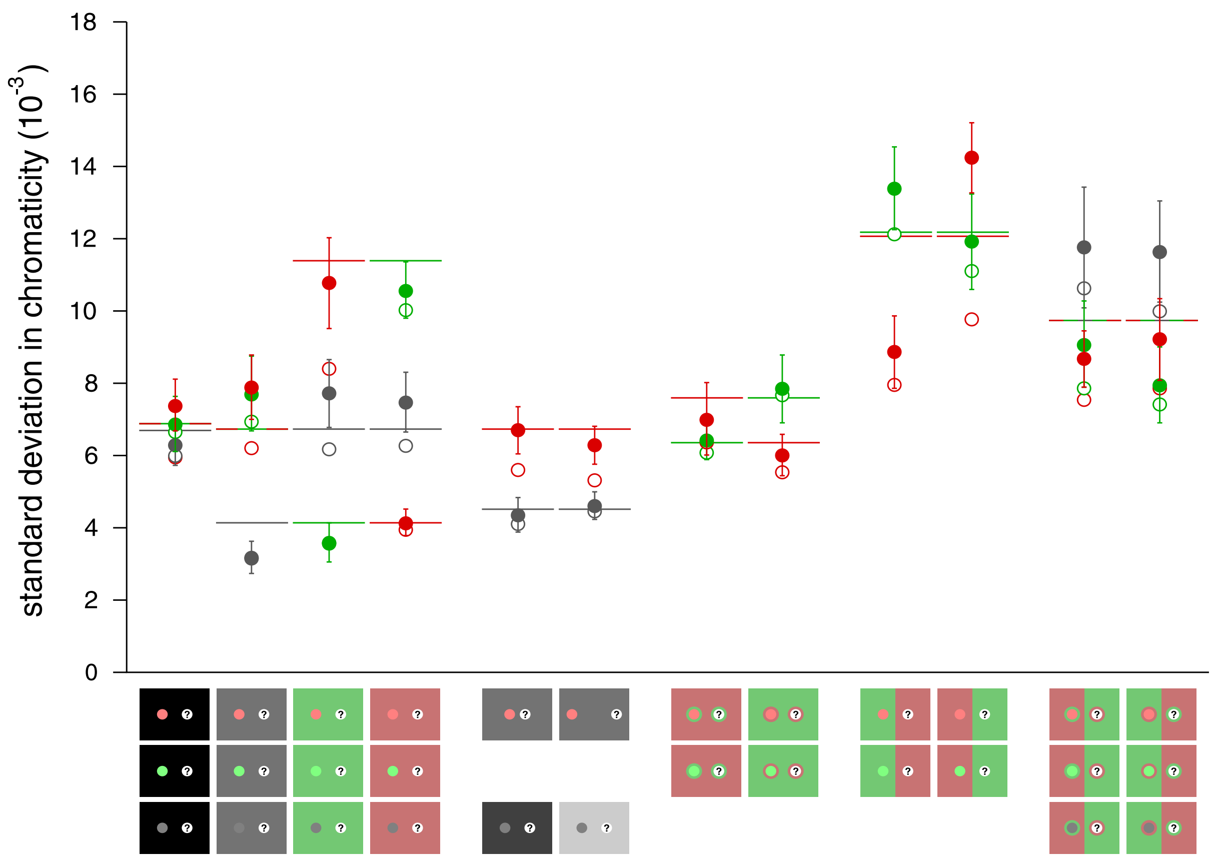

Fig. 3. Mean standard deviations in the colour direction of the logarithmic cone stimulation space in which we plot our data (see Fig. 2), for the settings in each of the 30 conditions (solid symbols; symbol colours correspond with the colour that is to be matched; error bars show standard errors across subjects). Open symbols show the corresponding values for the minor axes of the confidence ellipses. The horizontal lines are model fits. For further details about the conditions and measures see the text. (For interpretation of colour mentioned in this figure the reader is referred to the web version of the article.)

greenish disks on a reddish background, or reddish disks on a greenish background. The standard deviations are very similar for reddish or greenish disks on a uniform grey background, as for grey disks on a uniform reddish or greenish background. Thus, the standard deviations on a uniform background are as one would expect if the precision depended on the contrast at the disks' borders.

Second, the precision with which matches are made is not only determined by the colour contrast at the disks' borders. The standard deviation is (obviously) not zero when there is no colour contrast between the disks and the background. Moreover, although the colour contrast at the disks' borders is identical (zero) for the grey reference on a dark background and for the grey reference on a grey background, the standard deviation is considerably larger for the dark background. That this is due to the luminance contrast at the borders (rather than the background luminance) is evident from the fact that the standard deviation is similar for the light and dark grey backgrounds with matched contrast (grey symbols in second of the five sets of symbols in Fig. 3). The standard deviation at this intermediate luminance contrast is between the values for the high (dark background) and low (grey background) contrast.

Third, the standard deviations in the set colour for reddish and greenish reference disks are not larger on the dark background than on the grey one, so a high luminance contrast does not simply give rise to more variability. The precision in matching the disks is less dependent on the disks' colour when the luminance contrast is high, suggesting that the high luminance contrast at the disks' borders reduces the extent to which the colour contrast at those same borders influence the perceived colour; i.e. that less weight is given to matching the colour contrast at the border. When the contrast is only with a 0.5° reddish or greenish rim, and the rest of the background is the other colour, the standard deviation also depends to a much smaller extent on the border contrast (third set of symbols in Fig. 3). Although the greenish disks with greenish rims and the reddish disks with reddish rims were still matched slightly more precisely than the greenish disks with reddish rims and the reddish disks with greenish rims, all four conditions had quite a similar standard deviation to those on the dark background. These findings indicate that the weight given to matching the colour contrast at the disks' borders cannot be the same for all scenes.

Fourth, the standard deviations for asymmetric backgrounds are larger than those for symmetric backgrounds. Although this seems intuitively logical, in terms of local cone contrast and colour contrast at borders there is no reason to expect more variability. We attribute the larger standard deviations to variability in the extent to which the subjects rely on border contrast (σ_w in Eq. (4)). Since it is reasonable to expect σ_w to increase when w increases (for small values of w), the slightly smaller standard deviations for asymmetric backgrounds with rims surrounding the disks (rightmost set of symbols in Fig. 3) suggests that w (and thereby simultaneous colour contrast) is smaller in this condition.

Fifth, the separation between the two disks does not influence the accuracy of the match (red symbols in second set of symbols in Fig. 3). This is consistent with the perceived colour of each disk only depending on the local cone ratio and the border ratio. It is tempting to consider this as evidence against a more sophisticated spatial analysis or against the notion that the two disks are compared directly, but this is only a valid argument if the alternatives predict that performance will drop with increasing separation. If, for instance, the two disks are primarily compared across eye movements, then a larger separation just means that people need to make larger saccades.

Finally, there are some findings that are inconsistent with our model and assumptions. The colour contrast at the border of the disk of which the colour is set appears to have a stronger influence on the variability of the match than does the contrast at the border of the reference disk. Thus, for asymmetric backgrounds, the errors are smaller when the reference disk has a large colour contrast at its borders than when the other disk does. Obviously the model summarised in Eq. (4) cannot account for this asymmetry because it treats the two disks identically. Another example is that for some reason the variability for asymmetric backgrounds is particularly large for grey disks (see grey symbols in last set of data in Fig. 3). Without the data for these grey disks we may have proposed that border contrast is determined with respect to the average colour within 1° beyond the borders, so that both a reddish rim surrounded by a greenish area and a greenish rim surrounded by a reddish area are more or less equivalent to a uniform grey background. That would explain why the matches were almost as precise for reddish and greenish disks on such backgrounds (see third and last sets of data in Fig. 3) and why this precision was similar to that for the same disks on a grey background. We chose a width of 0.5° because we expected the border contrast to mainly depend on the colour within that distance of the disk (Brenner & Cornelissen, 1998). If we were mistaken about this, so that the backgrounds with rims can be considered to be approximately equivalent to a grey background, we would expect to have found exceptionally small standard deviations for the grey disks on asymmetric backgrounds with rims, rather than the exceptionally large ones that we found. Our model predicts similar standard deviations for grey disks to those for reddish and greenish disks. Thus, we have no explanation for the exceptionally large standard deviations for the grey disks in this condition.

Fig. 4 shows the average systematic errors that our subjects made in each condition. For symmetric backgrounds there is no reason to expect any bias, and indeed there is almost no bias. There may be a very slight tendency to exaggerate the colour that one is setting, but we will ignore it. For asymmetric backgrounds we expect relying on border contrast to give rise to systematic errors, as indeed

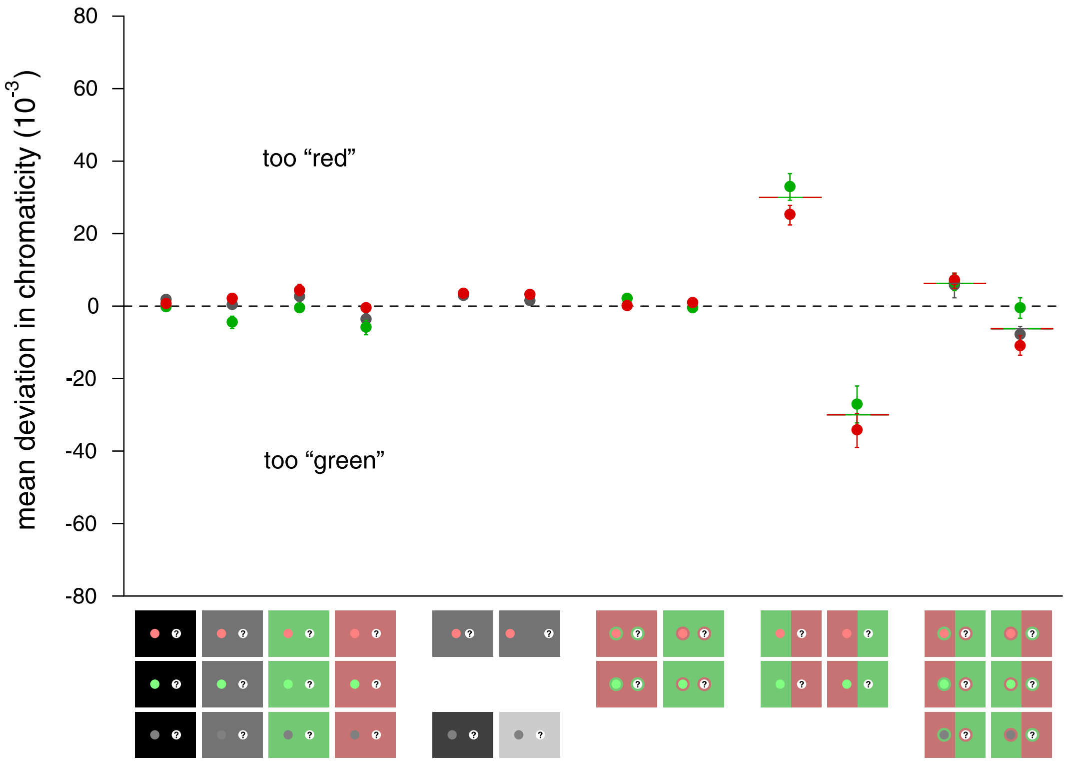

Fig. 4. Mean systematic errors in the colour direction of the logarithmic cone stimulation space in which we plot our data (see Fig. 2), for the settings in each of the 30 conditions (symbol colours correspond with the colour that is to be matched; error bars show standard errors across subjects' mean values). The horizontal lines in the asymmetric conditions are the average values that we use in our model (for the symmetric conditions the model always assumes a value of zero). Note the different scale than in Fig. 3. For further details about the conditions and measures see the text. (For interpretation of colour mentioned in this figure the reader is referred to the web version of the article.)

it does. Considering the difference in colour between the reddish and greenish backgrounds (Δ_B is about 0.14) we can estimate that the weight given to the border contrast (w) is 0.21 for the asymmetric background and 0.062 for the asymmetric background with rim (averaged across all colour combinations; see lines in Fig. 4). The smaller value of w for the background with rim is consistent with our interpretation of the smaller standard deviations in this condition in the fourth point mentioned above.

3.2. Luminance

Fig. 5 shows the average standard deviation in the luminance direction (see Fig. 2) for each condition (solid symbols). The standard deviations in the direction of the major axis of the fit ellipses are also shown for comparison (open symbols). The latter values must obviously be at least as high as the former. The variability is clearly mainly in luminance because the two measures are almost identical. The pattern in Fig. 5 is different from that of Fig. 3 (as obviously also are the values themselves: note the different axes in the two figures). Large standard deviations were found when the luminance contrasts at the disks' borders were large: for the dark background (leftmost symbols) and the matched high contrasts (grey symbols in the second set). The luminance contrast is also generally larger for reddish disks than for greenish ones (because their luminance is higher and the background is darker than the disks), and the standard deviations show a similar tendency. However luminance contrast alone cannot explain why (for instance) the variability for red disks on a uniform green background is larger than for the matched high contrast disks (because the luminance contrast at the borders of the latter is much higher). Performance was generally more variable for asymmetric than for symmetric backgrounds, in accordance with the proposal that there is variability in the weight given to contrast (σ_w).

Fig. 6 shows the average systematic errors in matching luminance. For symmetric backgrounds there is no reason to expect any bias, but it is evident that subjects tend to set a too high luminance. This is not caused by a skewed distribution of settings, because the same bias is evident in the median settings (not shown). It could nevertheless be introduced by our choice of colour space (in particular the logarithmic transformation from mouse coordinates to cone stimulation) because when moving the mouse to make ones settings a too high luminance may be less conspicuous than a too low one (perhaps because most of the targets in question are brighter than their backgrounds). Another possibility is that the asymmetry is somehow related to the asymmetry in fixation of the two targets (Cornelissen & Brenner, 1995). If we consider the average value set in symmetrical matching as the baseline

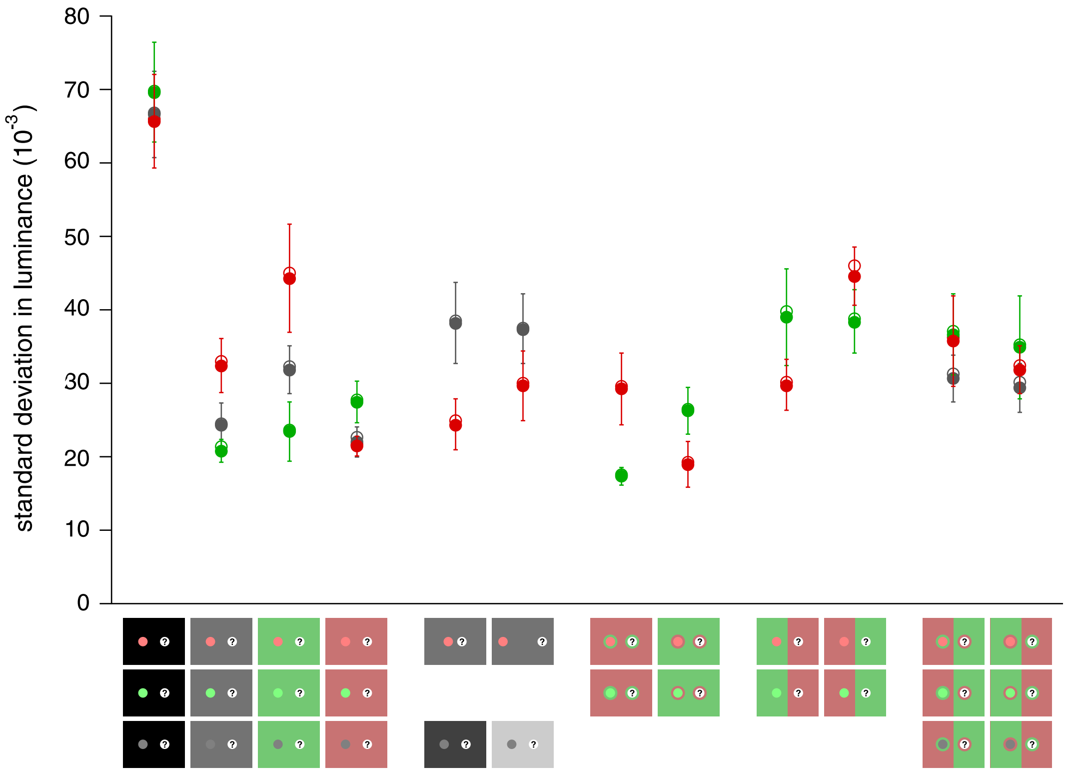

Fig. 5. Mean standard deviations in the luminance direction of the logarithmic cone stimulation space in which we plot our data (see Fig. 2), for the settings in each of the 30 conditions (solid symbols; symbol colours correspond with the colour that is to be matched; error bars show standard errors across subjects). Open symbols show the corresponding values for the major axes of the confidence ellipses. Note the different scale than in Fig. 3. For further details about the conditions and measures see the text. (For interpretation of colour mentioned in this figure the reader is referred to the web version of the article.)

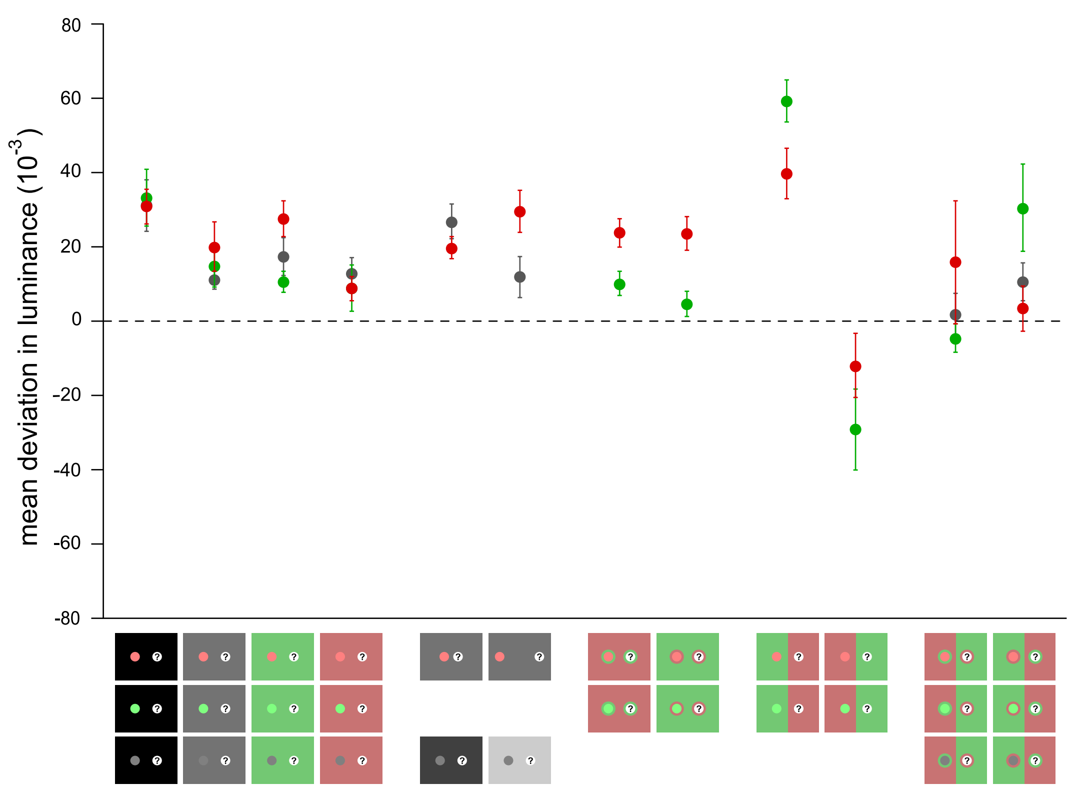

Fig. 6. Mean systematic errors in the luminance direction of the logarithmic cone stimulation space in which we plot our data (see Fig. 2), for the settings in each of the 30 conditions (symbol colours correspond with the colour that is to be matched; error bars show standard errors across subjects' mean values). For further details about the conditions and measures see the text. (For interpretation of colour mentioned in this figure the reader is referred to the web version of the article.)

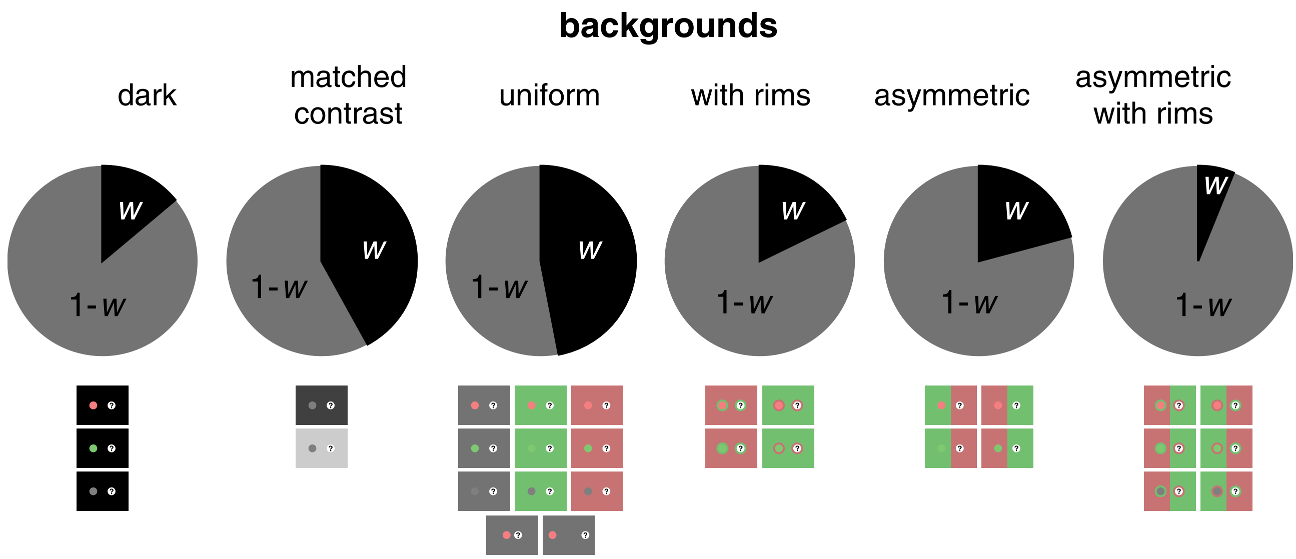

Fig. 7. Estimated contribution of border contrast to the perceived colour (dark sections of pie charts; w) for the six kinds of backgrounds. For asymmetric backgrounds the two values of w were determined from the systematic errors (Fig. 4). For symmetric backgrounds the four values of w were obtained by fitting our model to the data. (For interpretation of colour mentioned in this figure the reader is referred to the web version of the article.)

(rather than the correct value), we see that the systematic error in matching the luminance with asymmetric backgrounds is of about the same magnitude as it is in matching the colour (Figs. 4 and 6 are on the same scale). Note that for our choice of stimuli and colour space the difference in luminance between the reddish and greenish backgrounds is the same as the difference in colour (Δ_B). Thus, if our choice of colour space is appropriate then the same weight (w) may be given to the border contrast for both colour and luminance.

3.3. Fitting the model

Fitting Eq. (4) to the data represented by the solid symbols in Fig. 3 gave us the following values for the eight parameters: $\sigma_L = 0.0055$, $\alpha = 0.11$, $w = 0.14$ for the dark background, $w = 0.42$ for the matched high contrast backgrounds, $w = 0.47$ for the uniform backgrounds, $w = 0.18$ for the uniform backgrounds with a rim, $\sigma_w = 0.070$ for the asymmetric background (with $w = 0.211$ as determined from the systematic error), and $\sigma_w = 0.045$ for the asymmetric background with rim ($w = 0.062$). The horizontal lines in Fig. 3 show the values of σ_S (from Eq. (4)) for these parameters. Although Eq. (4) clearly does not capture all the details of the data, the fit is quite reasonable. Fig. 7 shows the six values of w: four from the fit and two based on the systematic errors.

Obviously a better fit could be obtained by not restraining the value of σ_L to be the same for all colours, by not assuming that judgments for the two disks are equivalent, and by not assuming a simple proportionality between colour contrast and its uncertainty. On the basis of our data there are reasons to believe that none of these assumptions are strictly valid. However the fact that we can fit the data with what we consider to be reasonable values for the parameters (as will be discussed in the next section) supports the general idea that the perceived surface colour is a compromise between the local colour and the contrast at the surface's borders (Brenner & Cornelissen, 1991).

4. Discussion

4.1. The main assumptions

We had to make many assumptions to model the data. One assumption is supported by the results: the value of σ_L seems indeed to be more or less independent of **L** itself within the range of colours used in this study. The variability was very similar both for the three target colours on backgrounds of the same colour and for the three target colours on the dark background (Fig. 3). A substantial difference in σ_L between the three colours would have led to a clear difference in variability between the differently coloured targets in at least one of these cases. The assumption that σ_B increases with **B** itself is supported by the matches made on the differently coloured uniform backgrounds, but the extent to which the increase is linear and independent of the variability in **L** is impossible to tell from our data. The assumption that the value of w, which is responsible for accounting for the differences between the conditions, is the same for all of the uniform backgrounds is inconsistent with our proposal that its value depends on the contrast within the scene, because the colour contrast between the target and the background is clearly smaller when the targets and background are the same colour. Nevertheless our simple assumptions can give quite a good account of the results. A real test of the model will require a quantitative prediction of how w depends on the scene.

4.2. The values of the parameters

It is impossible to judge whether the values of σ_L and α are reasonable because we have no independent way of judging them. The values of w (Fig. 7) are easier to evaluate. For instance, we expected the value of w to be smaller when there is a large luminance contrast at the target's border, because the magnitude of chromatic induction is smaller when there is a substantial luminance contrast at the target's border (Brenner & Cornelissen, 2002). And indeed, we find that the weight given to colour contrast at the border (w) is smaller for the dark grey background (90% luminance contrast) than for the normal grey background (about 10% contrast), with an intermediate value for the two matched contrast backgrounds (about 50% contrast). However, the weight is not simply proportional to the luminance contrast. Moreover, the weight clearly also depends on other aspects of the scene. For instance, if the background is split into two colours, or if the colour at the disk's outer border is only present in a 0.5° rim that is surrounded by another colour, then the weight given to border contrast is reduced from almost 50% to about 20%. For asymmetric backgrounds with a rim the weight is reduced further still: to about 6%. These findings are consistent with evidence that colour contrast throughout the whole scene can influence the extent to which people rely on border contrast (Barnes et al., 1999; Brenner et al., 2003). The values of σ_w are reasonable in that they are not larger than the weights themselves. However they are quite large in comparison with the weights. This implies that if our assumptions are correct, the weights are more flexible than we have hitherto assumed. That could account for the many differences between subjects and between studies, but unfortunately it also makes it less simple to judge whether the values of w themselves are reasonable.

4.3. Colour and luminance

Most of the variability in our subjects' matches was in luminance (correlated errors for *l*- and *m*-cones), in accordance with thresholds for detecting both slow modulations of cone stimulation (Noorlander et al., 1981) and the presence of increments of monochromatic light on a bright background (Sperling & Harwerth, 1971) being lowest when they were based on colour. For some of our stimuli, in particular where the standard deviations in luminance are high, the sensitivity to luminance is probably even lower than is suggested by our results, because subjects could not vary the *s*-cone stimulation. We restricted our subjects to two dimensions because doing so makes it much easier for the subject to find the correct setting and for us to analyse the data. However, keeping the *s*-cone stimulation constant at the correct value means that if subjects set too low values of *l*- and *m*-cone stimulation (i.e. a too low luminance) the *s*-cone stimulation is relatively strong, so the target looks bluish. Similarly, trying to set a too high luminance makes the target look yellowish. Thus what we here call the luminance direction is actually a combination of luminance and (relative) *s*-cone stimulation. This may account for some of the unexpected values in Fig. 5.

4.4. Spatial aspects

Fig. 3 shows that the weight given to border contrast (w) when combining local cone comparisons (**L**) with comparisons across borders (**B**) is not only selected to minimize the total variance (van Beers, Sittig, & Denier van der Gon, 1999; Ernst & Banks, 2002). If it had been then the weight would not depend on whether the matching was made on a symmetric or an asymmetric background. Apparently the likelihood of **L** and **B** giving reliable information about the surface's colour is also considered. This likelihood can be estimated from various statistics within the image. For instance, if the scene is very colourful, the surfaces near the surface of interest are likely to be coloured, so it is less likely that contrasts at the latter surface's borders will provide reliable information about its colour. And indeed, the influence of the direct surrounding in asymmetric colour matching is smaller if there are large colour contrasts within the scene (Barnes et al., 1999; Brenner et al., 2003; Shevell & Wei, 1998; Wachtler et al., 2001).

The fact that the value of w that we estimated was quite similar for asymmetric backgrounds as for symmetric backgrounds with rims, suggests that the weight given to border contrast is determined by simple scene statistics, rather than by a detailed consideration of the layout, because of course relying on border contrast is much more suitable for symmetric backgrounds. This has the important implication that the value of w could be determined by low-level (possibly retinal) mechanisms alone. However, the fact that adding rims to the asymmetric display reduced the value of w further still suggests that not only the range of colours but also the layout is important (or at least the number of edges, despite evidence to the contrary; Amano et al., 2005; Brenner et al., 1989; Valberg & Lange-Malecki, 1990).

In our proposal, we assume that the weights sum to one. The finding that surfaces look less saturated when the surrounding is colourful (Brown & MacLeod, 1997; Whittle, 1992) suggests that this may not be the case. The colourful surrounding may decrease the weight given to border contrast (**B**), without increasing the weight given to the local cone ratio (**L**) correspondingly. It is difficult to tell how such a change in weights would influence the variability, because although decreasing the total weight should reduce the variability, variability in the amount of reduction (equivalent to the role of σ_w in Eq. (4) for asymmetric backgrounds) may increase the variability. At present we therefore see no simple way to test such a hypothesis.

In Section 1 we mentioned the possibility that double-opponent cells are responsible for the influence of the local border contrast (**B**). However our model is in no way specific to this neuronal substrate. For instance, photoreceptor sensitivity could change in response to the colour of the background (Chichilnisky & Wandell, 1995) to optimize the resolution of each kind of cone, in which case it is evident that the lowest variability will be found when the target is similar to the background (i.e. when **B** is small). If this is the mechanism that underlies our results then the adaptation must be regulated quite locally, because the variability is largely determined by the colour within a small rim surrounding the target (the smallest variability is found when the target is the same colour as the rim rather than the same colour as the rest of the background; see third set of data in Fig. 3). An extreme possibility (in terms of adaptation being responsible for our results) is that photoreceptor adaptation spreads to nearby parts of the retina through small eye movements (which are needed to prevent the image from fading; Martinez-Conde, Macknik, Troncoso, & Dyar, 2006). If this is so then w indicates the extent to which such adaptation influences the signal from the target, the variability in w is the result of different viewing patterns on different trials, and the larger variability for asymmetric targets is simply a consequence of the different local backgrounds (and therefore adaptation) near the two targets. However, photoreceptor adaptation alone would predict that the variability would be largest when the background was dark (followed by the two conditions with about 50% luminance contrast) because that is when the change in cone stimulation across the targets' borders is largest, which is not what we find. Whatever the neuronal mechanism (or combination of mechanisms), we propose that the result is a weighted average of the light from the target itself and the change in the light near the target's border.

4.5. Colour constancy

The ability to judge how well surfaces reflect different colours from the light reaching our eyes, while the latter is the product of properties of the surface and of the illumination, is fundamental to colour vision (D'Zmura & Lennie, 1986; Hurlbert, 1996; Land, 1983). The kinds of mechanisms that we here propose for dealing with this issue could be implemented early in visual processing (Dacey & Packer, 2003; Hood, 1998; Kamermans, Kraaij, & Spekreijse, 1998). But is this enough to achieve normal levels of colour constancy, or is a more complete interpretation of the scene required, considering such factors as highlights, edges of shadows, mutual reflections, likely distributions of surface colours, likely colours of the illumination, and so on (see Smithson, 2005)? Relying on ratios between the stimulation of different kinds of cones ensures that the perceived colour is independent of the level of illumination, because doubling (for instance) the intensity of the illumination doubles the stimulation of both kinds of cones, so the ratio remains the same. However, when the spectral composition changes, the ratio of stimulation of different kinds of cones changes. The ratio between the ratios of stimulation of different kinds of cones across surface boundaries is more or less independent of the chromaticity of the illumination (Brenner & Cornelissen, 1991; Foster et al., 1997; Land & McCann, 1971), but it depends on the colours at both sides of the boundary so that the apparent colour of a surface depends on the colours of surrounding surfaces (Brenner & Cornelissen, 1991). This limits the extent to which one can rely on such ratios of ratios. According to our model the level of colour constancy that is achieved is directly related to the value of w, being complete for $w = 1$ (relying entirely on the ratios of ratios) and absent for $w = 0$ (ignoring the background altogether).

Under certain conditions colour constancy is known to reach levels of more than 80% (e.g. Kraft & Brainard, 1999). The highest weight given to the comparison across borders (w) in the present study was 0.47, which is not enough to account for such high levels of colour constancy. Probably the value of w would have been higher without the large luminance contrast at the edge of the screen (beyond the screen the room was very dark). However it is also certain that relying on border contrast (the extent of which is quantified by w) is not the only mechanism that contributes to colour constancy. The sensitivities of cones in the fovea change in accordance with the light coming from the surfaces that one is looking at, so some time after the illumination changes the changes in sensitivity will have compensated for the change in illumination (Von Kries, 1905). This method of achieving colour constancy is not perfect, because looking at a coloured surface for some time will influence subsequent judgments, just as a coloured local background influences one's judgments when relying on border contrast. Moreover, the speed of adaptation is critical because it should be fast enough to deal with natural changes in illumination, but not so fast that surfaces' colours constantly appear to change as one looks around. However, the human visual system surely relies on this mechanism too to some extent to achieve colour constancy.

In our model, an overall change in one kind of cone's sensitivity is equivalent to changing all the values of **L** (leaving **B** unaltered). In our matching task subjects were free to look back and forth between the disks (and presumably did so; Cornelissen & Brenner, 1995), so that the disks' images fell onto the same part of the retina. Thus even if the sensitivity of certain cones changed, this will have influenced the appearance of both disks in the same way. Matching surfaces in this manner is therefore a good way to evaluate the role of border contrast in colour vision. In asymmetric matching tasks, instructing subjects to fixate rather than to look back and forth between the disks can increase the extent to which the background influences the perceived colour considerably (Cornelissen & Brenner, 1991). Thus if our subjects did not only compare the disks across eye movements, the systematic errors for the asymmetric backgrounds may include some contribution of adaptation, so that our estimates of w may be slightly too high in these conditions. All these possibilities, together with the weight given to border contrast depending on the statistics of the scene, probably explain why human colour constancy is so robust and yet so difficult to model.

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